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The Shrubs of Indiana in Their Local and General Distribution by Physiographic Divisions

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THE SHRUBS OF INDIANA IN THEIR LOCAL AND GENERAL DISTRIBUTION ACCORDING TO PHYSIOGRAPHIC DIVISIONS

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The mesophytic deciduous forest is the climax type of flora in Indiana. The trees typify the dominant life-form of such a community, but the shrubs and herbaceous plants which go to make up the undergrowth have an important bearing on the nature of the vegetation as a whole. Within each climax formation there are numerous physiographic areas in which differences in vegetation are associated primarily with differences in topography and soil character. In Indiana there are six such areas, each with its distinctive floras (6, 11, 15). Lindsey (12) has made a study of the trees of Indiana, dealing with their distribution within the state in natural botanical areas and outside the state in their wider distribution by larger physiographic units. The present paper involves a study of the shrubs following the manner of the study of trees made by Lindsey.

LOCAL AND GENERAL DISTRIBUTION

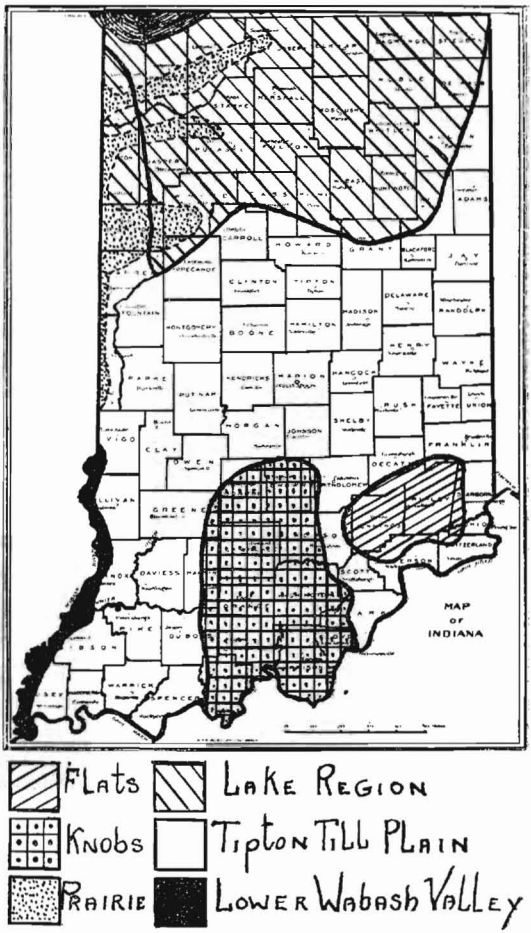
The shrubs of Indiana listed are the 212 species, varieties and forms which Deam (8) recognizes as occurring outside of cultivation within the state. Their distribution follows the ranges fixed by Deam, supplemented by the Butler University Catalogue of Indiana Plants, which records by counties all published records for each species. Where the range of a species has been enlarged to include more botanical areas than those given by Deam, it is starred and the collector given credit in a footnote (Table I). The nomenclature used is that of Deam's second edition of the Shrubs of Indiana. Whenever a conflict exists among workers concerning either the taxonomy or distribution of a species, the authority of Deam is given precedence. Since Indiana is divided into ninety-two counties and since these counties fall into six major botanical areas as indicated by Deam (7, 8), the local range of a species is determined first by counties and afterwards by botanical areas.

On the basis of the facts concerning the topography and geology of Indiana, Coulter and Thompson (3) divided Indiana into seven botanical regions. Deam (6) differentiated the botanical areas of Indiana according

to habitats having distinctive floras. In his later works (7, 8), he has delimited six well marked forestal areas in Indiana, modifying in some respects the divisions of Coulter and Thompson and his own earlier subdivision. Since these forestal areas have been followed in this study, Map 1 shows the outline of each area.

MAP 1

DEAM'S BOTANICAL AREAS OF INDIANA



DISTRIBUTION BY BOTANICAL AREAS

Maps were prepared which showed county distribution of the 212 species, and from these a list of the species occurring in each of Deam's botanical areas was prepared. Table I gives the location of species by botanical areas, the number of species in each area and the percentage in each area of the total number of shrubs found in the state.

TABLE I

SHRUBS OF INDIANA AND THEIR LOCATION BY BOTANICAL AREAS

NAME OF SPECIES	REGION OF LOCATION[1]						
	AA	L	TP	P	LWV	K	F
Alnus rugosa (Du Roi) Sprengel		x	x			x	
Amelanchier humilis Wiegand		x					
A. humilis x Amelanchier lævis Wiegand		x					
Amorpha canescens Pursh		x	x	x			
A. fruticosa L.		x	x		x	x	
Ampelopsis cordata Mx.			x		x	x	
Andromeda glaucophylla Link		x					
Aralia spinosa L.			x			x	x
Arctostaphylos uva ursi var. coactilis Fernald and MacBride		x					
Aristolochia tomentosa Sims.					x		
Aronia floribunda (Lindley) Spach		x	x				
A. melanocarpa (Mx.) Ell.		x	x			x	x
Ascyrum hypericoides L.			x			x	
Benzoin æstivale (L.) Nees	x						
Betula pumila L.		x					
B. pumila var. glandulifera Regel		x					
XB. purpusii Schneider		x					
Bignonia capreolata L.					x	x	
Bumelia lycioides (L.) Gaertn.						x	
Campsis radicans (L.) Seemann	x						
Ceanothus americanus L.	x						
C. ovatus Desf.		x					
Celastrus scandens L.	x						
Celtis pumila var. deamii Sarg						x	
Cephalanthus occidentalis L.	x						
[2]C. occidentalis var. pubescens Raf.		x	x		x	x	
Chamædaphne calyculata (L.) Moench		x					
Cornus alternifolia L. f.	x						

[1]Explanation of columu headings: AA, All Areas; L, Lake Area; TP, Tipton Till Plain; P, Prairie Area; LWV, Lower Wabash Valley Area; K, Knobs Area; F, Flats Area.

[2]Peattie (17) extends the range of this species in Indiana into the Lake Area.

Name of Species	Region of Location						
	AA	L	TP	P	LWV	K	F
C. amomum Mill.			x			x	
C. asperifolia Mx.	x						
C. baileyi Coulter and Evans		x					
C. obliqua Raf.	x						
C. racemosa Lam.	x						
C. rugosa Lam.		x	x				
C. stolonifera Mx.		x	x				
C. stricta Lam.			x		x	x	
Corylus americana Walter	x						
Cratægus alnorum Sarg.		x					
C. arduenna Sarg.		x					
C. barrettiana Sarg.			x				
C. brainerdi Sarg.		x					
C. coujuncta Sarg.		x					
C. dewingii Sarg.			x				
C. crecta Sarg.			x				
C. gracilis Sarg.			x				
C. gracillipes Sarg.		x					
C. hillii Sarg.			x				
C. ignea Sarg.		x					
[3]C. intricata Lange		x	x				
C. meticulosa Sarg.						x	
C. palustris Ashe			x				
C. parviflora Sarg.		x					
C. rotundifolia Moench.		x					
C. rutila Sarg.		x					
C. sejuncta Sarg.		x					
C. spathulata Mx.					x		
C. straminea Beadle		x					
C. trahax Sarg.			x				
Diervilla lonicera Mill.		x	x				
Dirca palustris L.		x	x			x	x
Epigæa repens L.		x	x			x	
Evonymus americanus L.						x	x
E. atropurpureus Jacq.	x						
E. obovatus Nutt.		x	x	x		x	x
Gaultheria procumbens L.		x	x			x	
Gaylussacia baccata (Wang.) K. Koch		x	x			x	x
G. baccata var. leucocarpa (Porter) Fernald		x	x				
Grossularia cynosbati (L.) Mill.		x	x	x		x	x
G. hirtella (Mx.) Spach.		x					
G. missouriensis (Nutt.) Coville and Britton		x	x			x	x
Hamamelis virginiana L.	x						

[3]Range extended into the Lake Area by a report of Peattie (17).

Name of Species	Region of Location					
	AA	L	TP	P	LWV	K	F
Hudsonia tomentosa var. intermedia Peck		x					
Hydrangea arborescens L.	x						
H. arborescens var. deamii St. John			x		x	x	
H. arborescens var. oblonga T. and G.	x						
Hypericum kalmianum L.		x					
H. prolificum L.	x						
Ilex decidua Walter			x		x		
I. verticillata (L.) Gray	x						
Juniperus communis var. depressa Pursh		x	x				
Kalmia latifolia L.						x	
Lonicera canadensis Marsh.		x					
L. dioica L.		x					x
L. dioica var. glaucescens (Rydberg) Butters		x	x				
L. dioica var. glaucescens forma dasygna (Rehder) Deam		x				x	x
L. japonica Thunb.			x			x	x
L. prolifera (Kirchner) Rehder		x	x				
Myrica asplenifolia L.		x					
Nemopanthus mucronata (L.) Trel.		x					
Parthenocissus quinquefolia (L.) Planchon	x						
[4]P. vitacea (Knerr) Hitchc.		x	x			x	
Phoradendron flavescens (Pursh.) Nutt.					x	x	x
Physocarpus opulifolius (L.) Maxim.	x						
P. opulifolius var. intermedius (Rydberg) Robinson		x					
Potentilla fruticosa L.		x	x				
Prunus angustifolia Marsh.		x	x			x	x
P. pumila L.		x					
P. virginiana L.		x	x			x	x
P. virginiana var. demissa (Nutt.) Torr.		x	x				
Ptelia trifoliata L.	x						
P. trifoliata var. deamiana Nieuwland		x					
P. trifoliata forma mucronata (Nieuwland) Deam.		x					
Rhamnus alnifolia L'Heriter		x					
R. caroliniana Walt.						x	
R. caroliniana var. mollis Fernald						x	
R. lanceolata Pursh.		x	x			x	
Rhus canadensis Marsh.		x	x			x	x
R. copallina L.	x						
R. glabra L.	x						
R. glabra var. borealis Britton		x					
R. toxicodendron L.	x						
R. typhina L.		x	x		x		
R. vernix L.		x	x		x	x	

[4]Price and Welch (19) report this species for Monroe County, which extends it into the Knobs Area.

Name of Species	Region of Location					
	AA	L	TP	P	LWV	K	F
Ribes americanum Mill	x						
R. americanum var. mesochora Nieuwland		x					
Rosa blanda Ait		x	x				
R. blanda var. glandulosa Schuette		x					
R. blanda var. hispida Farwell		x					
R. carolina L.	x						
[5]R. carolina var. glandulosa (Crepin) Farwell		x	x			x	
R. carolina var. sabulosa Erlanson		x					
R. deamii Erlanson				x			
R. lyoni Pursh.	x						
R. obovata Raf.		x	x				
R. palustris Marsh.	x						
R. relicta Erlanson				x			
R. rubiginosa L.		x	x		x	x	
R. rudiuscula Greene				x			
R. setigera Mx.	x						
R. setigera var. tomentosa T. and G.	x						
R. suffulta Greene				x			
Rubus allegheniensis Porter.	x						
R. alumnus Bailey		x			x		
R. argutus Link	x						
R. flagellaris Willd.	x						
R. frondosus Bigel.	x						
R. hispidus L.		x	x				x
R. hispidus forma pleniflorus Nieuwland		x					
R. idæus var. canadensis Richardson		x					
R. idæus var. strigosus (Mx.) Maxim.		x					
R. occidentalis L.	x						
R. occidentalis forma pallidus (Bailey) Robinson		x	x				
R. odoratus L.			x			x	
Salix adenophylla Hook.		x					
S. bebbiana Sarg.		x	x				
S. candida Flügge		x					
S. candida var. denudata Andersson		x					
S. cordata Muhl.		x	x	x			x
S. discolor Muhl.	x						
S. discolor var. eriocephala (Mx.) Andersson	x						
S. glaucophylla Bebb		x					
S. humilis Marsh.	x						
S. longifolia Muhl.	x						
S. longifolia var. wheeleri (Rowlee) Schneider		x	x			x	
S. longipes Shuttleworth						x	
S. lucida Muhl.		x					

[5]Range extended into the Lake Region by a report of Peattie (17).

Name of Species	Region of Location						
	AA	L	TP	P	LWV	K	F
S. lucida var. intonsa Fernald		x					
S. pedicellaris Pursh.		x	x				
S. petiolaris J. E. Smith		x	x				
S. sericea Marsh.		x	x		x	x	x
S. serissima (Bailey) Fernald		x					
S. tristis Ait.		x	x	x		x	
Sambucus canadensis L.	x						
S. canadensis forma atroflavula House		x					
S. pubens Mx.		x	x				
S. pubens var. zanthocarpa Nieuwland		x					
Shepherdia canadensis (L.) Nutt.		x					
Smilax bona-nox L.						x	
S. glauca Walt.			x		x	x	x
S. hispida Muhl.	x						
S. rotundifolia L.	x						
Sorbus subvestita Greene		x					
Spiræa alba DuRoi	x						
S. tomentosa L.		x	x	x			x
Staphylea trifolia L.	x						
Styrax americana Lam.		x			x	x	
Symphoricarpos orbiculatus Moench			x		x	x	x
Taxus canadensis Marsh			x				
Vaccinium arboreum Marsh						x	
[a]V. canadense Kalm		x	x				
V. corymbosum L.		x					
V. corymbosum var. amœnum (Ait.) Gray		x					
V. corymbosum var. atrocarpum Gray		x					
V. corymbosum var. pallidum (Ait.) Gray		x					
V. macrocarpon Ait.		x	x				
V. oxycoccus L.		x					
V. pennsylvanicum Lam.		x					
V. pennsylvanicum var. nigrum Wood		x					
V. stamineum L.			x			x	x
V. stamineum var. neglectum (Small) Deam						x	
V. vacillans Kalm		x	x			x	x
V. vacillans var. crinitum Fernald		x	x			x	
Viburnum acerifolium L.		x	x			x	x
V. acerifolium forma ovatum Rehder							x
V. affine Bush		x	x				
V. affine var. hypomalacum Blake		x	x				
V. cassinoides L.		x					
V. lentago L.	x						
V. molle Mx.			x				x

[a]Range extended into the Lake Area by a specimen in the Butler University Herbarium.

Name of Species	Region of Location						
	AA	L	TP	P	LWV	K	F
V. prunifolium L.	x						
V. pubescens var. deamii Rehder			x			x	x
V. pubescens var. indianense Rehder			x			x	x
V. rufidulum Raf.						x	x
V. trilobum Marsh.		x					
Vitis æstivalis Mx.	x						
V. cinerea Engelm.		x	x		x	x	
V. cordifolia Mx.	x						
V. labrusca L.		x	x		x		x
V. rubra Mx.					x		
V. vulpina L.	x						
[1]V. vulpina var. syrticola Fernald and Wiegand.		x	x				
Zanthoxylum americanum Mill.	x						
Total species per area	48	119	78	10	21	55	30
Per cent per area of the 212 total shrubs	23	56	37	5	10	26	14
Per cent per area of the 163 total trees of Indiana— Lindsey (12)	10	71	65	14	66	65	45

To this list of shrubs for Indiana by Deam (8), other authors have added species (13, 17, 18). Some of these species are: *Hamamelis virginiana orbiculata* Nieuwland, *Hudsonia tomentosa* Nutt, *Rubus floricomus* Blanchard, *R. idaeus* var. *anomalus* Arrhenius, *R. randii* (Bailey) Rydberg, *R. recurvans* Blanchard, *Vaccinium atrococcum* (Gray) Heller and *V. corymbosum* var. *glabrum* Gray. Since these shrubs either are not included or given specific rank by Deam, they are omitted from the list for this discussion. Recently, a new shrub, *Rubus phoenicolasius* Maxim, was collected in Crawford county and added to the Butler University Herbarium. This species has been introduced into America from Japan and is an escape in Crawford county. However, it is becoming established in open places on the hills near Marengo Cave and in time may be added to our Indiana flora.

Deam (8) has excluded sixty-eight species of shrubs from the Indiana list for want of satisfactory evidence to warrant their inclusion. Of these, some bave ranges far beyond our area, some have been reported as escapes, and tbe reports on others have been too indefinite. The species of Berberis, injurious to wheat by the black stem rust, have been excluded because these shrubs will not become members of our flora since

[1]Range exteuded into the Tipton Till Plain by a specimen from Parke County in the Butler University Herbarium.

an effort is being made to exterminate them. For a further discussion of the excluded species, reference should be made to Deam (8).

Table I shows that the Lake area has the highest number of shrub-species of any of the areas, due no doubt to the unusual number of Lake region exclusives and to the fact that many of the species occurring in one or more of the other areas occur also in the Lake region.

The Tipton Till Plain follows in the number of species it possesses, while the Knobs, Flats, Lower Wabash Valley and Prairie areas follow with decreasing percentages. A comparison of the shrubs with the trees is given in percentages at the end of Table I. It is seen that the tree species of Indiana occur in the largest numbers also in the Lake area, while the Lower Wabash Valley, the Tipton Till Plain and Knobs, the Flats and the Prairie areas follow with decreasing percentages. It is interesting also to note that 23 per cent of the shrub species and only 10 per cent of the tree species occur in all areas.

From the figures the Prairie region would appear to be practically shrubless until it was remembered that species listed for all areas occur in the Prairie region also. Welch (28) has made a study of one of the prairie counties and finds that these areas in Indiana are in the transition zone between deciduous forest and prairie. The prairie type of vegetation is decidedly dominant, but trees and shrubs are found in groves in habitats supplied with sufficient water for their maintenance and in situations high enough to have been protected from the annual prairie fires. The Lower Wabash Valley region is also limited in species, due to the fact that this is a very narrow strip of land subject to inundation by the Wabash river. Such an area naturally would contain only those species which could adjust themselves to such a variable habitat.

These numerical values of the regions are not absolute, because areas are not sharply defined. A species may be found plentifully in one area, but it may be able to survive across the boundary of its characteristic area, and even though only a few shrubs of this species exist in this contiguous area, it is counted in both areas. Where shrubs occur only in counties near the border-line of an area, it is difficult to determine whether they should be placed in one or both areas. This was especially true of the Cratægi. Such a small amount of information could be gleaned concerning their habitats that it was difficult to decide in a number of cases whether a species belonged in the Lake region or in the Tipton Till Plain. If a more accurate distribution were possible, it is certain that there would

be changes in these figures. Deam (6) has pointed out, "The number of plants found in a state depends largely upon the intensity with which they are sought." This, no doubt, is true of the shrubs in the different botanical areas. In all of the areas there are species either exclusive or characteristic of the area.

THE LAKE REGION

In Table I it will be noted that sixty species are limited to the Lake area. This region contains more exclusives than all other areas combined. The general distribution of all these species has not been worked out by any one, but the known wider distribution of these exclusives is characteristically extraneous to the north, northwest and northeast, although some have western and some have eastern and southeastern extensions along the Appalachians. Three species, *Ribes americanum* var. *mesochora*, *Rubus hispidus* forma *plentiflorus* and *Sambucus pubens* var. *xanthocarpa* have no distribution reported except that for the immediate vicinity of the Lake region in Indiana.

Most of these shrubs find the bogs, swamps and sand dunes suitable habitats, while a number find the open woods of this area a suitable environment. Of the 51 shrubs whose habitats have been noted by collectors, 51 per cent prefer the swamps and bogs, 31 per cent the sand dunes, while 33 per cent are found in open woods. Of those found in the open woods, 14 per cent are found also in the bogs, swamps or sand dunes. The species found in the extreme habitats of bog, swamp and sand dunes may linger here at the southern edge of their range until their position is no longer tenable, due to the invasion of the oaks and the climax forests into these habitats (4, 5).

KNOBS AREA

Of the fifty-five species of shrubs found in the Knobs area in the unglaciated region in Indiana, ten were found to be exclusive to the area (Table I).

The wider distribution of the shrubs of this area is heaviest toward the south and southeast. Plants preferring a southern habitat can be found in this region in the warm protected ravines. However, *Kalmia latifolia* is restricted to the ledges and upper parts of the ridges in the Knobs area. This species is found nowhere else in Indiana, but it shows

an affinity for the far northeast in its wider distribution. This gives evidence that both here and in eastern and southeastern mountains, conditions characteristic of more northern areas apparently pertain. In this area, then, plants preferring either a cooler or a warmer climate find a suitable environment. Coulter and Thompson (3) state that the plants of this region are peculiar in that species on one side of a knob may be found growing in a climate similar to that of Northern British America, while on the other side of the same knob plants may be found flourishing luxuriantly whose natural climate is found in Florida or Mississippi.

THE LOWER WABASH VALLEY AREA

The Lower Wabash Valley region is less distinctive than either the Lake or Knobs areas in the number of exclusives possessed. Of the twenty-one shrubs listed for the Lower Wabash Valley, only four are exclusive, *viz., Aristolochia tomentosa, Crataegus spathulata, Vitis rubra* and *Foresteria acuminata.* This latter species often appears as a small tree, but in Indiana it is usually shrublike. No doubt the shrubs of this region have found here a climate very similar to that of southern latitudes in the low grounds and protected ravines, since most of them find the lowlands a suitable habitat. They are southern, southeastern and southwestern in their general ranges.

The Lake region exclusives are on the southern limit of their ranges in northern Indiana. The Knobs and Lower Wabash Valley exclusives are on the northern limit of their ranges in southern Indiana. Cowles (5) states that the behavior of species at the edge of their ranges may be regarded as extremely significant of the present trend of migration. The exclusives of these areas seem to indicate that the shrubs, like the trees, are entering Indiana from the south and southeast and are leaving by the north and northeast (12).

THE FLATS AREA

The Flats area is less distinctive in regard to its shrub flora than any of the other areas, since it possesses no exclusive species.

THE TIPTON TILL PLAIN

Seven species of Cratægus are listed as exclusives of the Tipton Till Plain. These species are reported for only one county each and most of them for counties so near the boundary between regions that it is difficult to ascertain to which region each species really belongs. When more reports have been made on these species, it may be found that they are not all Tipton Till Plain exclusives. Little is known about their general distribution.

Taxus canadensis is a glacial relic and is exclusive to this area. It is found only in Montgomery and Parke counties in Indiana and grows usually under hemlock trees or near them. While it is geographically exclusive to this area, its physiographic relations are not at all characteristic of the physiography of the area.

THE PRAIRIE AREA

The Prairie area is distinctive in having the smallest percentage of shrubs of any botanical area. There are four exclusive species: *Rosa deamii, R. relicta, R. rudiuscula* and *R. suffulta. R. relicta* and *R. suffulta* are not found in the Prairie as this area is delimited on Map 1, but they are considered as Prairie exclusives because they occupy prairie habitats in Indiana and have been reported in no other environment in this state. *Rosa rudiuscula* and *R. suffulta* are on the eastern limit of their ranges in the Prairie area in Indiana. *R. suffulta* extends throughout the western prairies, while *R. rudiuscula* is extraneous to the southwest. The general distribution of *R. deamii* and *R. relicta* is not known.

SPECIES WITH RANGE LIMITS IN INDIANA AND WHICH OCCUPY MORE THAN ONE BOTANICAL AREA IN INDIANA

Of the shrubs exclusive to different botanical areas of Indiana, those of the Knobs area range over the most restricted territory, while those characteristic of Tipton Till Plain and Prairie areas range over the most extensive territory. The great majority of Indiana shrubs are intraneous in varying degrees in their wider distribution, but the species with verified range limits listed in the tables as being exclusive to an area are

extraneous. Other species having ranges which terminate in Indiana, but which are not confined to a single botanical area, are given in Table II.

TABLE II

Species Which Occupy More Than One Botanical Area in Indiana and Whose Ranges Terminate in Indiana

Name of Species	Direction of General Distribution							
	N	E	NE	NW	W	S	SE	SW
Amorpha canescens				x	x	x		x
Ampelopsis cordata		x			x	x	x	x
Aralia spinosa		x				x	x	x
Aronia floribunda	x	x	x	x			x	
A. melanocarpa	x	x	x	x			x	
Ascyrum hypericoides		x			x	x	x	x
Bignonia capreolata		x				x	x	
Cephalanthus occidentalis var. pubescens						x		x
Cornus rugosa	x	x	x	x				
C. stricta		x				x	x	x
Crataegus intricata		x	x		x		x	
Diervilla lonicera	x	x	x	x			x	
Evonymus americanus		x	x		x	x	x	x
Hydrangea arborescens		x			x	x	x	
H. arborescens var. deamii		x			x	x		x
H. arborescens var. oblonga		x			x	x	x	
Ilex decidua		x			x	x	x	x
Juniperus communis var. depressa	x	x	x	x	x			
Parthenocissus vitacea	x	x	x	x	x			x
Phoradendron flavescens		x				x	x	x
Potentilla fruticosa	x	x	x	x	x			x
Rosa blanda	x	x	x	x	x			
Rubus alumnus					x			
R. odoratus		x	x				x	
Salix bebbiana	x	x	x	x	x			
S. longifolia var. wheeleri	x	x	x	x	x			
S. pedicellaris	x	x	x	x				
Sambucus pubens	x	x	x	x	x		x	
Smilax glauca		x	x		x	x	x	x
Styrax americana		x				x	x	
Viburnum molle		x			x	x	x	x
V. rufidulum		x			x	x	x	x
Vitis cinerea					x		x	x
Total (33)	12	29	16	13	21	17	21	16

MIGRATION, RELICS, ENDEMICS, DISJUNCTS AND COASTAL PLAIN SPECIES

During the past, successive waves of vegetation have passed over Indiana, due to the advance and retreat of the glaciers. Since the state lies in the central northern part of the country, it became the common meeting ground of postglacial migrations from various directions. Many warmth-loving plants were able to migrate before the cold, which came on gradually, while those of higher latitudes were driven in to take their places. With the return of warmer conditions, the ice cap retreated, permitting and compelling plants to move northward again. In these alternate movements, which may have taken place several times, relic species have been stranded in our present flora. Some of these are listed in Table III.

A number of species of Atlantic Coastal Plain affinity found a more or less continuous pathway for inland extension during this time. These plants may have migrated from three different sources: the Mississippi basin, from the Mohawk-Hudson outlet and the eastern Great Lakes, and from the Ottawa connective as shown by McLaughlin (14). It is possible that plants from the Mississippi basin have been carried upstream by marginal eddy currents, which may carry drift for considerable distances. Also, the flat sandy bottoms which once carried glacial streams, such as the Mississippi, would have been favorable to the development of shifting beds, sloughs and marginal lakes where plants could establish themselves on the borders. The recession of the last ice advance left the Great Lakes region open to occupancy by vegetation. At that time the sand barrens, swales and lagoons resulting from glaciation were far more extensive than at present. It is reasonable to imagine that the shores of the glacial lakes giving rise to the present Lake Erie and Lake Michigan were a series of lagoons, ridges, strands and low dunes harboring the newly migrated coastal plain and strand types. No doubt a connective formerly existed across the Grand River valley of southern Michigan. Glacial Lake Warren in the Erie basin extended eastward into the Finger Lakes district of New York. When the Grand River connective ceased to function, Glacial Lake Lundy in the Erie basin found an outlet eastward past the ice margin down the Mohawk and Hudson River valleys. A connective between the part of Glacial Lake Algonquin which lay in the Lake Huron basin and Champlain Sea in the St. Lawrence-Ottawa valleys was finally opened by the continued reces-

TABLE III

Relic, Endemic, Disjunct and Coastal Plain Species of Shrubs in Indiana

Name of Species	Relic	Endemic	Disjunct	Coastal Plain	General Direction of Migration: N	NE	NW	S	SE	E
Alnus rugosa				x		x			x	x
Andromeda glaucophylla	x				x	x	x			
Arctostaphylos uva-ursi var. coactilis	x				x	x	x			
Betula pumila	x				x	x				
Chamædaphne calyculata	x				x	x	x			
Cornus rugosa	x				x	x				x
Epigæa repens	x				x	x				
Hudsonia tomentosa var. intermedia	x			x		x				x
Hypericum kalmianum	x					x				
Juniperus communis depressa	x				x	x	x			
Myrica asplenifolia				x		x				x
Prunus pumila				x		x				x
Rhus toxicodendron				x		x		x	x	x
R. typhina				x		x		x	x	x
Salix adenophylla	x					x				
S. bebbiana				x		x				x
S. discolor				x		x				x
S. humilis				x		x		x	x	
S. petiolaris				x		x				x
Shepherdia canadensis	x				x	x	x			
Styrax americana			x	x				x	x	
Taxus canadensis	x				x	x	x			
Vaccinium macrocarpon	x			x	x	x			x	x
V. pennsylvanicum				x		x				x
Viburnum pubescens var. deamii		x								
V. pubescens var. indianense		x								
Total (26)	13	2	1	13	10	23	6	4	6	12

sion of the ice sheet to the north. Apparently, the pathway for the inland migration of the coastal plain flora was open sooner in the Hudson-Mohawk valley, since some plants indicate that they had followed the retreating ice front northward and later migrated up the Ottawa connective. It is altogether possible then that a species may be a glacial relic and a coastal plain species. While most coastal plain types are gradually dying out before the advance of the more aggressive floras, some species have spread to a greater or less extent in recent times wherever conditions favorable for their growth are found.

Table III lists species of shrubs which found a suitable environment

during the former extensive migrations of plants and have remained in our flora as relic, endemic, disjunct and coastal plain species. While endemics also may be relics and disjuncts may be coastal plain species, they are listed in different columns. The general direction from which these species may have migrated into the state is given also. No claim is made that this list is exhaustive. (3, 5, 6, 10, 11, 14, 16, 25, 26, 27.)

PHYSIOGRAPHIC AREAS

Since physiographic factors of habitat practically define the botanical areas within Indiana, a comparison of the shrubs in their wider distribution according to their physiographic location throughout the United States and parts of Canada seemed expedient. The topographically and edaphically determined habitats in the state have arisen during the course of physiographic development and have more or less definite relations to the larger physiographic features of the region. So natural areas were chosen rather than political divisions by states, because within an agreeable habitat a species may migrate freely regardless of specified state lines (15).

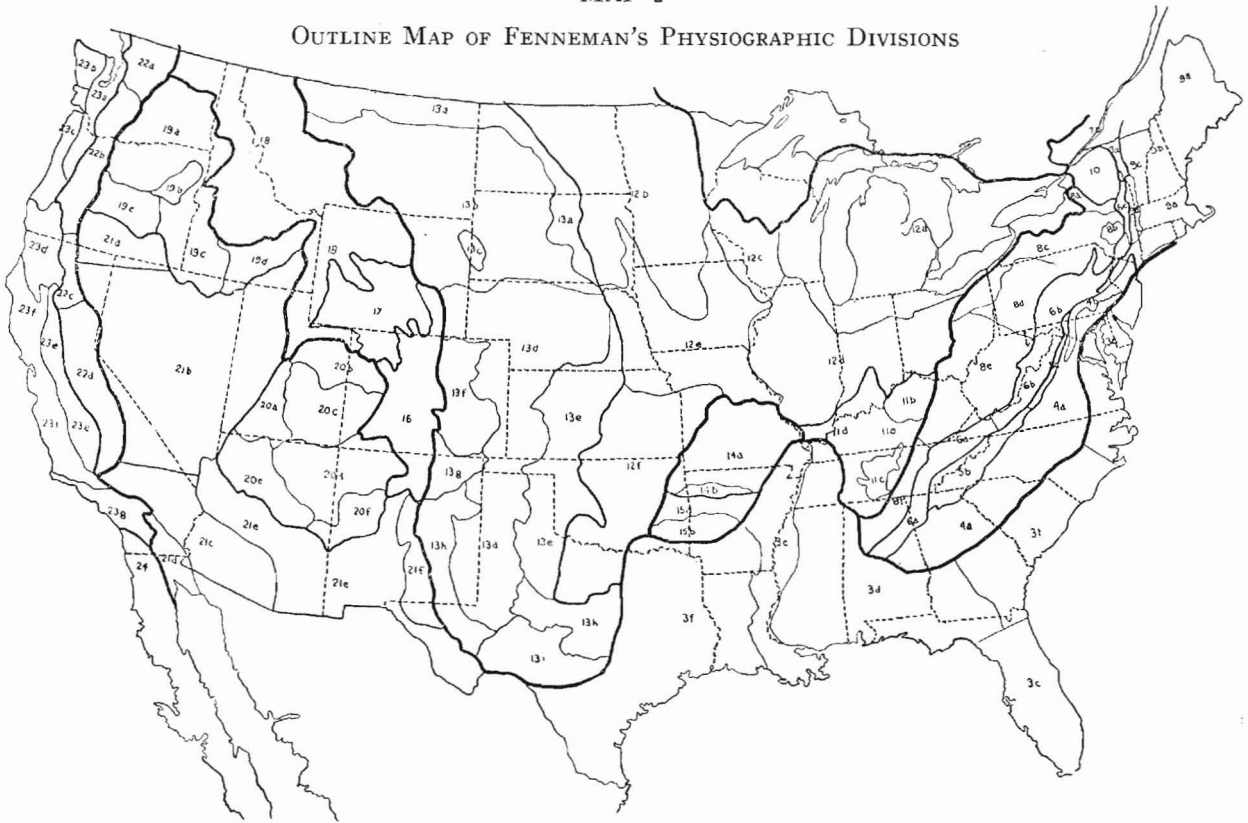
Fenneman (9) has divided the United States into eight strongly characterized parts called major divisions. The divisions are divided into units called provinces, units of the next smaller order being designated as sections. The major divisions are correlated with the great constructional events of geologic history. All orders of divisions rest ultimately on existing differences in topography and elevation, the differences considered being those which pertain to physiographic types and not merely to superficial appearance. This work of Fenneman, therefore, offers the best natural differentiation of areas for showing the physiographic distribution of the shrubs of Indiana. Map II shows these divisions in outline. For an enumeration of these divisions the paper by Lindsey (12) should be consulted.

PHYSIOGRAPHIC DISTRIBUTION

Of the 212 species of shrubs given by Deam (Table I), twenty-six are disregarded concerning their wider distribution, due to the fact that sufficient information could not be obtained which would fix their ranges to any reliable extent. The ignored species are as follows: *Amelanchier humilis* x *Amelanchier laevis*, *XBetula purpusii*, *Crataegus barrettiana*,

MAP 2

OUTLINE MAP OF FENNEMAN'S PHYSIOGRAPHIC DIVISIONS



C. conjuncta, C. gracilis, C. gracillipes, C. ignea, C. meticulosa, C. palustris, C. parviflora, C. rutila, C. sejuncta, C. trahax, Lonicera dioica var. *glaucescens* forma *dasygna, Prunus virginiana* var. *demissa, Ptelia trifoliata* var. *deamiana, P. trifoliata* forma *mucronata, Rosa blanda* var. *hispida, R. carolina* var. *sabulosa, R. deamii, R. relicta, Sambucus canadensis* forma *atroflavula, Vaccinium corymbosum* var. *atrocarpum, V. vacillans* var. *crinitum, Viburnum acerifolium* forma *ovatum, Vitis vulpina* var. *syrticola.*

For the 186 shrubs which remain, ranges were determined after Deam (8), Rosendahl and Butters (21), Britton and Brown (1), Small (24), Robinson and Fernald (20), Coulter and Nelson (2), a few species of Rosa by Rydberg (22) and some species of Cratægus by Sargent (23). If a check list of all shrubs appearing in each state in the United States could be obtained, no doubt the range of many shrubs would be extended. A large table was prepared which contained all the physiographic areas of Fenneman. After checking the entire range of each shrub, the number of species appearing in each province or section was totalled and its percentage of the entire number of 186 shrubs found. Percentage classes were found in order to compare the density of species of the different provinces and sections in this manner: Under per cent class No. 1 is listed the section containing between 91-100 per cent of the 186 shrubs; class No. 2, the provinces and sections containing between 81-90 per cent, and other classes in descending order of 10 per cent intervals, making ten classes in all. Table IV gives the percentage classes which show the result of this tabulation.

Map 3 shows by shadings the variations in density of the Indiana shrubs over their entire range. The shadings are representative and not absolute, because provinces and sections are not sharply divided and the ranges of all species are not yet accurately drawn. The map reveals the general distribution within the United States of all the Indiana shrubs.

The section of heaviest density with respect to number of species in Indiana falls in the Lake region (Fenneman's division 12a). Lindsey (12) found that the section of heaviest density for the trees included the following: Tipton Till Plain, Prairie, Lower Wabash Valley and the Flats (Fenneman's division 12d). The greater density of the shrubs in the Lake area is undoubtedly due to the presence of so many bogs and lakes which have not yet passed the shrub stage on their way toward the mesophytic forest climax. Further, it has been stated that many of the shrubs

TABLE IV

PERCENTAGE CLASSES FOR SHOWING THE VARIATIONS IN DENSITY OF THE DIFFERENT PHYSIOGRAPHIC DIVISIONS

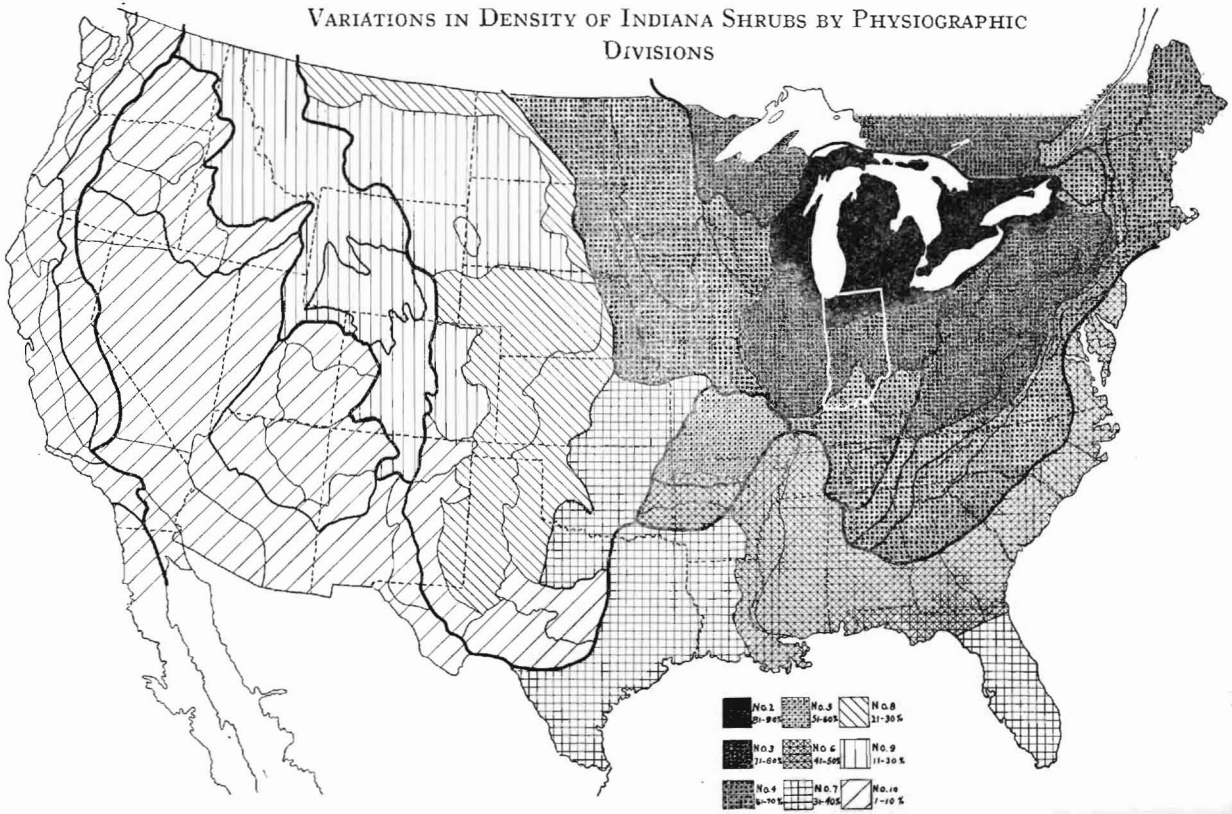
PER CENT CLASS	No.	PHYSIOGRAPHIC AREAS IN PERCENTAGE CLASS
91-100	1	None
81- 90	2	12a
71- 80	3	1; 6b; 8b; 8c, 8d, 8e; 12d
61- 70	4	4a, 4b; 5a, 5b; 6a, 6c; 7a, 7b; 8a, 8f; 9a, 9b, 9c, 9d; 10; 11a, 11b, 11c, 11d; 12b, 12c, 12e
51- 60	5	14a
41- 50	6	3a, 3b, 3d, 3e; 14b; 15a, 15b
31- 40	7	3c, 3f; 12f
21- 30	8	13a, 13d, 13e
11- 20	9	13b, 13c, 13f; 16; 17; 18
1- 10	10	13g, 13h, 13i, 13k; 19a, 19b, 19c, 19d, 19e; 20a, 20b, 20c, 20d, 20e, 20f; 21a, 21b, 21c, 21d, 21e, 21f; 22a, 22b, 22c, 22d; 23a, 23b, 23c, 23d, 23e, 23f, 23g; 24

characteristic of other areas also find suitable habitats in the Lake region, while in addition many typical bog and lake shrubs occur in the Lake era and not elsewhere. The real significance of the difference between location of areas of greatest density of trees on the one hand and shrubs on the other is the fact that much of the state outside of the Lake region has passed the shrub stage of succession into the tree stage toward the vegetational climax.

The area of heaviest density is surrounded by two density classes, numbers 3 and 4 of the descending order. Density class 3 surrounds the section of heaviest density except for parts at the east and west where density class 4 is contiguous. This means that only two lanes of different numerical value radiate from a common center. There is a somewhat definite correlation between a density class and its distance from the region of heaviest density, the density decreasing gradually with the distance to the south, southeast, southwest, and the distant west; very gradually to the north, northeast and northwest. For example, class number 6 is on the whole farther from the region of heaviest density than class number 5. All of the density classes present an irregular arrangement because of the abrupt ending of ranges and the irregular outlines of the sections and provinces. Only three classes, 5, 9 and 10, are central-

MAP 3

Variations in Density of Indiana Shrubs by Physiographic Divisions



ized and have a general direction of extension. Class 5, occupying the fifth heaviest density area, is southwestern; class 9 is middle western, and class 10 is far western. The remaining classes are not confined to a single direction. The shrubs of Indiana have their ranges most generally in the eastern half of the United States, but more shrubs than trees of Indiana have ranges in the western half of the United States, since the prairies do not present such a barrier to the shrubs as to the trees. Indeed, some of the shrubs serve as a connecting link between the deciduous forests of the east and the prairies of the west.

The distribution of Indiana shrubs, shown graphically on Map 3, is in accordance with physiographic affinity, since the physiographic range of a species indicates in a general way the type of minor physiographic or botanical area it occupies in Indiana. For example, the shrubs of the Lake region occupy similar physiographic regions in their wider distribution. Those of the Lower Wabash Valley occupy similar habitats to those of this area in their general distribution. The "all over" species in Indiana show no marked preference for certain physiographic areas in their wider distribution.

SUMMARY AND CONCLUSIONS

1. Twenty-three per cent of all Indiana shrubs are found in all the botanical areas. The percentage of the different botanical areas appear in this descending order: Lake region, Tipton Till Plain, the Knobs, the Flats, the Lower Wabash Valley and the Prairie regions.

2. The Lake region is especially distinctive in its possession of exclusives, having almost twice as many exclusives as all other areas combined.

3. Each species limited to one botanical area in Indiana is on the limit of its range and is extraneous in its distribution.

4. The extraneous species lie in four general directions from Indiana, and in each case the direction is usually in direct relation to the physiographic character of the botanical area in which the species is found, *viz.*, Lake region exclusives to the northeast; Knobs exclusives to the southeast; Lower Wabash Valley exclusives to the south; and Prairie exclusives to the west. These species, however, may have extensions in one or more adjoining directions.

5. Shrubs found in all areas of the state and most of those that are

characteristic of a particular botanical area are intraneous species and are well within their ranges in Indiana.

6. Fifty-six per cent of all Indiana shrubs have range limits in Indiana. Of these, 41 per cent are exclusives in one or other of the botanical areas and the remainder range in two or more areas, but not in all.

7. A number of relic, endemic and disjunct species are found among the shrubs of Indiana. These were left in our area by the advance and retreat of the glaciers.

8. The strongest affinity of Indiana shrubs for physiographic provinces, in part, or totally outside of Indiana, is to the north, northeast, and northwest. The weakest affinity is to the west, beginning with the Great Plains and continuing westward.

9. The physiographic provinces occupied by a species indicates in a general way the type of minor physiographic (botanical area) it occupies in Indiana.

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